Host Range of the Emerald Ash Borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) in North America: Results of Multiple-Choice Field Experiments

Andrea C. Anulewicz,[1,2,3] Deborah G. McCullough,[1,2] David L. Cappaert,[1] and Therese M. Poland[4]

ABSTRACT   Emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae), an invasive phloem-feeding pest, was identified as the cause of widespread ash (*Fraxinus*) mortality in southeast Michigan and Windsor, Ontario, Canada, in 2002. *A. planipennis* reportedly colonizes other genera in its native range in Asia, including *Ulmus* L., *Juglans* L., and *Pterocarya* Kunth. Attacks on nonash species have not been observed in North America to date, but there is concern that other genera could be colonized. From 2003 to 2005, we assessed adult *A. planipennis* landing rates, oviposition, and larval development on North American ash species and congeners of its reported hosts in Asia in multiple-choice field studies conducted at several southeast Michigan sites. Nonash species evaluated included American elm (*U. americana* L.), hackberry (*Celtis occidentalis* L.), black walnut (*J. nigra* L.), shagbark hickory [*Carya ovata* (Mill.) K.Koch], and Japanese tree lilac (*Syringa reticulata* Bl.). In studies with freshly cut logs, adult beetles occasionally landed on nonash logs but generally laid fewer eggs than on ash logs. Larvae fed and developed normally on ash logs, which were often heavily infested. No larvae were able to survive, grow, or develop on any nonash logs, although failed first-instar galleries occurred on some walnut logs. High densities of larvae developed on live green ash and white ash nursery trees, but there was no evidence of larval survival or development on Japanese tree lilac and black walnut trees in the same plantation. We felled, debarked, and intensively examined >28 m² of phloem area on nine American elm trees growing in contact with or adjacent to heavily infested ash trees. We found no sign of *A. planipennis* feeding on any elm.

KEY WORDS   *Fraxinus*, host range, oviposition preference, invasive pest, host selection

The adaptation of insect populations to their host plants involves two major classes of characters: (1) behaviors that influence the choice of a plant for feeding or oviposition and (2) physiological traits that affect the insects' growth and reproduction (Futuyma and Peterson 1985, Via 1986, Thompson 1988). Past studies have shown that host preference of adult females does not always correlate with larval performance and that some females will oviposit on hosts unsuitable for larval development (Thompson 1988). Because the vast majority of phloem-feeding and wood-boring larvae cannot disperse to alternate or more suitable hosts, oviposition choices by adult females are critical (Hanks et al. 1993). Many of these insects rely on olfaction to locate potential hosts that may be patchily distributed within forested areas (Haack and Slansky 1986). Survival of offspring is driven by host suitability rather than host preference, because larvae must feed and develop on the host chosen by the female (Hanks 1999).

Emerald ash borer (*Agrilus planipennis* Fairmaire), an Asian buprestid, was identified in July 2002 as the cause of widespread ash (*Fraxinus*) mortality in southeastern Michigan and Essex County, Ontario, Canada (Cappaert et al. 2005b). Additional populations have since been found across most of lower Michigan and in at least five additional states (www.emeraldashborer.info). As of 2007, an estimated 20 million ash trees in southeastern Michigan alone were dead or dying (www.emeraldashborer.info), and millions more trees were infested. *A. planipennis* was largely unknown outside Asia, and little information was available about its biology or ecology at the time of its discovery in North America (Cappaert et al. 2005b).

The life cycle of *A. planipennis* in North America is generally completed in 1 yr, although some individuals may require 2 yr to complete development (Cappaert et al. 2005a, Siegert and McCullough 2005, Siegert et

[1] Department of Entomology, Michigan State University, 243 Natural Science, East Circle Dr., East Lansing, MI 48824.

[2] Department of Forestry, Michigan State University, 243 Natural Science, East Circle Dr., East Lansing, MI 48824.

[3] Corresponding author: Department of Entomology, Michigan State University, 243 Natural Science, East Circle Dr., East Lansing, MI 48824 (e-mail: andreaa@msu.edu).

[4] USDA Forest Service, Northern Research Station, 1470 S. Harrison Rd., East Lansing, MI 48823.

al. 2007a). In Michigan, adult beetles emerge in May and June and feed on ash leaves during their 3- to 6-wk life span. Mating generally begins 5–7 d after emergence, and oviposition typically does not begin until after 2–3 wk of leaf-feeding (Bauer et al. 2004, Cappaert et al. 2005b). Each female may lay 30–60 eggs from late June to August. Eggs are laid individually on or just under the bark surface and inside bark cracks and crevices (Chinese Academy of Science 1986, Yu 1992, Bauer et al. 2004). Eggs hatch in ≈2 wk, and larvae feed in the cambium and phloem from late July to October. Larval galleries, which eventually score the outer sapwood, disrupt vascular tissue, ultimately girdling and killing the tree. Larvae pass through four instars (Cappaert et al. 2005a) and most overwinter as prepupal larvae ≈1 cm deep in the outer sapwood or in the bark of large, thick-barked trees (Cappaert et al. 2005b).

The native range of *A. planipennis* includes China, Japan, Korea, Mongolia, the Russian Far East, and Taiwan (Yu 1992, Jendek 1994). Limited reports from Asia suggest that *A. planipennis* functions largely as a secondary pest in its native range, generally occurring at low densities and attacking severely stressed or declining trees (Akiyama and Ohmomo 2000, Schaefer 2005, Williams et al. 2005, 2006). In North America, however, where ash species have no co-evolutionary history with this insect, *A. planipennis* has killed healthy, as well as stressed, green ash (*F. pennsylvanica* Marsh.), white ash (*F. americana* L.), black ash (*F. nigra* Marsh.), and blue ash (*F. quadrangulata* Michx.). Whether *A. planipennis* host preference or attack success varied among North American ash species was unknown at the time of its discovery.

There was also concern about whether nonash species could be attacked by *A. planipennis* in North America. In 1994, Jendek synonymized *A. marcopoli* Obenberger, *A. molco-poli* [sic!]: Miwa and Chujo, *A. feretrius* Obenberger, and *A. marcopoli* variety *ulmi* Kurosawa as *A. planipennis.* Reports and observations from China indicate that *A. planipennis* colonizes numerous *Fraxinus* spp., including *F. chinensis* Roxb., *F. mandshurica* Rupr., *F. pennsylvanica*, *F. rhynchophylla* Hance, and *F. velutina* Torr (Chinese Academy of Science 1986, Yu 1992, Liu et al. 2003, Zhao et al. 2005). In Japan, however, *A. marco-poli* and *A. marco-poli ulmi* reportedly attacked *Ulmus propinqua* Koidz (Kurosawa 1956). Other brief reports indicate hosts of *A. planipennis* subsp. *ulmi* in Japan, Korea, northern China, and Mongolia include *Juglans* spp., *Ulmus* spp., and *Pterocarya* spp., as well as *Fraxinus* spp. (Akiyama and Ohmomo 1997, 2000, Sugiura 1999).

North American congeners of trees reportedly attacked in Asia, such as American elm (*U. americana* L.), black walnut (*J. nigra* L.), and hickory (*Carya* sp.), are common in forests and landscapes across much of North America. In addition, other members of the ash family (Oleaceae), such as Japanese tree lilac (*Syringa reticulata* Bl.), are commonly used in landscape settings. To date, attacks on nonash trees have not been observed in North America. If *A. planipennis* were to attack additional species, however,

environmental and economic impacts would increase dramatically in North America. Given the extensive damage caused by *A. planipennis*, there is an urgent need to evaluate the susceptibility of other common landscape and forest trees that may serve as alternate hosts to *A. planipennis* in North America.

The primary goal of these studies was to determine if *A. planipennis* would land on or oviposit on species other than ash, and if so, whether larvae could successfully develop on nonash species. Alternate host species included North American congeners of species reportedly attacked by *A. planipennis* in Asia (American elm and hackberry [*Celtis occidentalis* L.] [both Ulmaceae], black walnut, hickory). Japanese tree lilac was also assessed because of its relatedness to ash and its wide use as a landscape tree. A second objective focused on whether host preference or suitability for *A. planipennis* development varied among common North American ash species.

We conducted several multiple-choice studies in the field to compare adult *A. planipennis* landing rates, oviposition, larval survival, and larval development on North American ash species and potential alternate host species. In 2003, we compared landing rates of adult *A. planipennis*, oviposition, and larval density among small logs of ash and alternate host species mounted on t-posts at four sites. We also debarked American elm trees growing adjacent to heavily infested ash trees in 2003 to determine whether any *A. planipennis* larval feeding occurred on the elms. In a second study, repeated annually from 2003 to 2005, we attached small logs of ash and alternate hosts to the trunk of ash trees in heavily infested sites where female beetles would have a high probability of encountering the logs. Egg and larval density were quantified on the logs each year. Finally, in 2004 and 2005, we evaluated larval density and development on young trees planted in a common garden and exposed to a high density *A. planipennis* population.

Materials and Methods

Study 1: Adult Landing, Oviposition, and Larval Development on Cut Logs Mounted on t-posts (2003)

Logs of six different species, including green ash, white ash, black walnut, shagbark hickory [*Carya ovata* (Mill.) K. Koch], American elm, and hackberry, were harvested from 8 to 10 apparently healthy trees of each species at Michigan State University's W. K. Kellogg Experimental Forest, Kalamazoo Co., MI, on 16 June 2003. Kellogg Forest was not known to be infested by *A. planipennis* as of early 2007. Logs were cut to ≈60 cm in length, and both ends were waxed to prevent desiccation. Log diameter ranged from 7.3 to 18.2 cm, with a mean of 13.1 ± 0.2 (SE) cm.

We set t-posts, 2 m tall, into the ground, ≈10 m apart at each study site (see below). A log was positioned vertically at the top of each t-post and attached with wire; approximately one half of the log extended above the top of the t-post. Logs were

set out in a randomized complete block design with four to eight blocks at each site (see below). There were a total of 24 logs per species; 1 damaged white ash log was not used (143 total logs). A section of black, plastic drain pipe, 12 cm in diameter and 60 cm long, was included in one half of the blocks as a control to see if *A. planipennis* adults would land on nonwoody material.

At each site, logs in 50% of the blocks, selected at random, were wrapped with clear, plastic, stretch wrap and covered with Tanglefoot. At the Eckles site, all logs were wrapped (109 logs total). Only the top half of the logs was covered with the sticky band, leaving the bark on the bottom half of the logs exposed for oviposition. All 16 of the drain pipes were similarly wrapped. Logs were checked weekly and adult beetles were counted and removed from the sticky bands from 17 June to 14 August 2003 to assess landing rates. Logs were stored outside until they were dissected from 5 November 2003 to 16 March 2004. Total surface area (outer bark) was calculated from the log length and circumference (outer bark). Logs were intensively examined (by one researcher), and the number of eggs found in 5 min of inspection was recorded. Bark was carefully peeled down to the wood using a drawknife. Number and stage of larvae were recorded and standardized by meter squared of log surface area.

Study Sites. The study was conducted at four sites where attributes such as the extent of canopy dieback, evidence of woodpecker predation on *A. planipennis*, and observations of adult beetles indicated that *A. planipennis* density was moderate to heavy. Six blocks were established at Bicentennial Park in Livonia, Wayne Co., along the border of an infested woodlot that surrounded an open field. An additional six blocks were established at Kensington Metropark, Livingston Co., MI, in an open field surrounded on two sides by infested woodlots. Eight blocks were established in unmowed areas of the Western Golf Course and Country Club in Redford, Wayne Co., MI, near live but presumably infested ash trees. Although many dying ash trees had been removed from the golf course in the preceding year, >25 infested ash trees remained on the course, and additional infested ash trees were in residential areas surrounding the course. At the Eckles Road yard in Plymouth Township, Wayne Co., MI, large quantities of infested ash logs from the surrounding area were stockpiled until they could be chipped, providing a source of newly emerged adult beetles during much of the summer. No live ash trees grew on the site or in the immediate vicinity. Four blocks were arranged linearly around the perimeter of the yard.

Study 2: Oviposition and Larval Development on Cut Logs Positioned in Ash Trees (2003, 2004, 2005)

2003. Ten black walnut and 10 American elm logs were harvested from three to four trees of each species at Hudson Mills Park, Washtenaw Co., MI, on 9 June 2003 and stored outdoors under shade. Ten green ash logs were harvested from three trees at Kellogg Forest on 23 June 2003. Log diameter ranged from 9.2 to 14.6 cm, with a mean of 11.9 ±0.3 cm.

Three logs, one of each species, were attached to the trunk of a large, infested green ash tree, 5–7 m above ground (one group per tree) using a randomized complete block design. Logs were attached vertically with plastic cable ties, rotating around the circumference of the stem, such that the top of the lower log overlapped slightly with the log above it. A group of logs was attached to each of five green ash trees at Bicentennial Park. On three of the trees (≈25 cm diameter at breast height [DBH] and 17 m height) growing 5–10 m inside the edge of a woodlot, we placed logs just below the canopy. Logs were attached to the trunk at mid-canopy on two additional trees (≈20 cm DBH and 12 m height) growing in the open between a recreation field and a parking area. Logs were also attached, just below the canopy, to five green ash trees (≈25 cm DBH and 20 m height) in a wooded area at Kensington Metropark. Logs remained in place from 24 June to 14 August and were dissected as described above between 26 August and 4 September 2003.

2004. Eighteen green ash, nine white ash, nine black walnut, and nine American elm logs were harvested from three to six trees of each species at Kellogg Forest, and nine blue ash logs were harvested from three trees in Superior Township, Washtenaw Co., on 15 June 2004 (54 logs total). All trees appeared healthy at the time of harvest. Log diameter ranged from 9.3 to 16.7 cm, averaging 13.0 ± 0.3 cm. Two study sites, both in wooded areas with numerous white ash, were established at Parker Mills and Marshall parks in Ann Arbor, Washtenaw Co., MI. At each park, nine white ash trees (18 trees total, ≈15–20 m in height, DBH averaging 17.0 ± 0.6 SE cm) were selected in a large forested area.

Groups of three logs were attached to each of the nine white ash at each site using an incomplete block design. Each group consisted of a green ash log (control), a second ash log (white or blue ash), and a nonash log (elm or walnut). Green ash logs were always placed in the middle position of the group, and the two other logs alternated between the top and bottom positions. Logs remained in place from 17 June to 11 August and were dissected between 17 September and 10 December 2004.

2005. In 2005, we attached both green and white ash logs to both green and white ash trees. Forty green ash, 40 white ash, and 13 black walnut logs were harvested from 4 to 15 trees of each species at Kellogg Forest, and 14 black ash logs were harvested from four trees in a woodlot at Sharon Hollow, Washtenaw Co., MI, on 13 June 2005. Thirteen blue ash logs were harvested from four trees at the Strait Creek Nature Preserve, an uninfested site in Adams Co., OH, on 10 June 2005. All trees appeared healthy at the time logs were collected. Logs (120 total) ranged from 48 to 66 cm and averaged 12.5 ± 0.2 cm in diameter.

Ten *A. planipennis*–infested ash trees were selected in each of four sites in the greater Ann Arbor area (40 trees total). Two sites consisted of open-grown street

trees; the Wellington neighborhood had green ash trees and the Windemere neighborhood had white ash trees. The other two sites were in wooded areas; the Dickens Woods site had white ash trees and the Kensington Metropark site had green ash trees. Tree height ranged from 12 to 18 m with a mean DBH of 31.0 ± 1.9 cm.

One group of three logs was attached to each tree using an incomplete block design. Each group consisted of a green ash log, a white ash log, and a third log that was either black ash, blue ash, or black walnut. On 15 and 16 June 2005, logs were attached in random order along the trunk of the trees. Logs remained in place until 17 August 2005 and were debarked between 30 September and 1 December 2005.

Study 3: Larval Density and Development on Live Trees (2004, 2005)

2004. On 12 May 2004, green ash, white ash, Japanese tree lilac, and black walnut balled-and-burlapped trees delivered from an Illinois nursery were planted at the Matthaei Botanical Gardens, Washtenaw Co., MI. Ten blocks of trees, with a mean DBH of 5.8 ±0.1 cm, were established in a randomized complete block design (40 trees total). Trees were planted in an open field, 3 m apart, in five rows of eight trees. Trees were mulched, and drip line irrigation was installed for frequent watering.

Screen cages constructed around the lower stem of each tree for a related study served to exclude wild *A. planipennis* from the lower 1 m of the stem (Anulewicz et al. 2006). The upper, uncaged portions of the trees, however, remained exposed to wild *A. planipennis* emerging from numerous ash trees in the vicinity. The nursery trees remained in place throughout the 2004 *A. planipennis* flight season and were harvested after larvae had finished feeding. Four of the 10 blocks of trees were randomly selected and harvested on 1 and 2 November 2004. Trees were cut just above the cage, returned to the laboratory, and dissected between 1 November and 10 December 2004. The remaining six blocks were cut and dissected in March 2005. In the laboratory, the main stem and all branches >0.5 cm in diameter were carefully peeled down to the wood. Number and stage of *A. planipennis* larvae were recorded. On average, an area of 0.55 ± 0.06 m^2 was debarked on each tree.

Each tree was assigned to one of three classes based on a qualitative estimate of bark texture. Low bark roughness indicated that the bark was smooth, with very few to no cracks or crevices. Trees with medium bark roughness had a moderate abundance of cracks and crevices suitable for *A. planipennis* oviposition. Trees with high bark roughness had abundant cracks and crevices.

2005. The study was repeated in 2005 using the same four species supplied by the same Illinois nursery. Root balls left from the 2004 trees were removed, and new trees were planted in the existing holes on 13 May 2005. Trees were again covered with wood mulch and

drip line irrigation was reinstalled. Trees had a mean DBH of 7.1 ± 0.2 cm.

The lower 1-m portions of trees were again protected by screen cages to exclude wild *A. planipennis.* Upper, uncaged portions of the trees were harvested and debarked two blocks at a time in December 2005 and January 2006 using the same methods as in 2004.

Study 4: American Elm Survey

We encountered an opportunity to determine if *A. planipennis* would oviposit or develop on American elm trees when suitable ash host material became scarce. A high-density *A. planipennis* population was present in a wooded area of Bicentennial Park in 2003. This area was dominated by green ash and American elm trees growing in close proximity to each other. In several cases, the trunks of ash and elm trees were in direct contact or even intertwined with each other. The rapidly decreasing availability of live ash trees in the park and surrounding areas and the abundance of elm and green ash trees growing adjacent to each other suggested that this would be an optimal site to look for evidence of *A. planipennis* larval feeding in American elm.

On 19 December 2003, nine American elm trees, each growing within 5 m of highly infested green ash trees, were selected for sampling. Three of the nine elms had trunks that were physically in contact with the trunks of infested ash trees. Two of the elm trees had >200 cm^2 of bark on the trunk directly in contact with bark on the trunk of ash trees that had been completely girdled by *A. planipennis* larvae. Distance of elms from the nearest ash ranged from 0 to 4.6 m, with a mean of 2.8 ± 0.3 m. Mean DBH for the 28 green ash trees closest to the nine elms was 25.8 ± 1.4 cm; mean elm DBH was 15.6 ± 1.3 cm. On each of these ash trees, we removed bark from a 30 by 30-cm area 1.5 m above ground to estimate the proportion of phloem consumed by *A. planipennis* larvae. Twenty-five of the 28 ash trees died in 2003. The remaining three trees died in 2004.

The nine elm trees were felled and carefully debarked with drawknives to look for *A. planipennis* galleries. Four of the elms were completely peeled, and 50–80% of the bark on the trunk and branches of the other five trees was removed.

Voucher specimens of *A. planipennis* (Voucher 2006-05) were collected and deposited in the Michigan State University Entomology Museum in East Lansing, MI, on 13 July 2006.

Statistical Analysis

All variables were tested for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965) and residual plots. Landing rates and gallery density for logs attached to ash trees in 2005 were normalized by $\log(x + 1)$ and square-root$(x + 1)$ transformations, respectively (Ott and Longnecker 2001). Gallery density for logs attached to ash trees was analyzed using the MIXED procedure for mixed models in SAS sta-

Table 1. Total and mean ± SE no. *A. planipennis* adults, eggs per square meter, and galleries per square meter for logs and drain pipes attached to t-posts at four field sites in 2003

	Green ash	White ash	American elm	Black walnut	Hickory	Hackberry	Drain pipe
Adult landing rates[a]							
No. logs	19	18	18	18	18	18	16
No. logs with adults	16	14	16	15	11	12	7
Total no. adults	112	121	86	133	83	49	25
Mean no. adults	5.9 ± 1.3a	6.7 ± 2.5a	4.8 ± 1.3a	7.4 ± 2.9a	4.6 ± 1.3a	2.7 ± 0.7ab	1.1 ± 0.5b
Eggs							
No. logs	24	23	24	24	24	24	
No. logs with eggs	12	14	5	3	2	12	
Total no. eggs	79	120	8	23	3	23	
Mean no. eggs/m²	14.1 ± 3.9ab	21.7 ± 6.5a	1.2 ± 0.5bc	3.2 ± 2.0bc	0.5 ± 0.4c	3.7 ± 0.9abc	
Larval galleries							
No. logs with galleries or feeding attempts	8	11	0	4	0	0	
Total no. galleries	217	215	0	0	0	0	
Mean no. galleries/m²	39.6 ± 17.1a	36.5 ± 14.8a	0b	0b	0b	0b	
Total no. feeding attempts	0	0	0	51	0	0	
Mean no. feed. attempts/m²	0	0	0	7.6 ± 7.0	0	0	

Within rows, means followed by the same letter are not significantly different (Kruskal-Wallis test and nonparametric multiple comparisons procedure; $P < 0.05$).

[a] At each site, 50–100% of the logs had a sticky band to capture adults.

tistical software (PROC MIXED; SAS Institute 2003) with site type (street tree or woodlot tree), tree species (green or white ash), and log species as fixed effects and tree number as a random effect. Differences among treatment means were tested as unplanned comparisons and multiple comparison tests were applied only when overall analysis of variance (ANOVA) was significant ($P < 0.05$). Two- and three-way ANOVAs were performed to determine significant effects between site type (woodlot versus street trees), among tree species, and among log species using SAS statistical software (PROC MIXED; SAS Institute 2003). When significant differences occurred, the Fisher protected least significant difference (LSD) test was used to evaluate species differences (Ott and Longnecker 2001).

Other variables, including eggs per square meter and galleries per square meter, could not be normalized by transformations. For non-normal variables, Friedman's two-way nonparametric ANOVA was used to assess differences among sites and species (PROC NPAR1WAY; SAS Institute 2003). The nonparametric Wilcoxon rank sum (S statistic) or Kruskal-Wallis (H statistic) tests were applied to assess whether egg and gallery densities differed among species within sites or whether bark roughness affected gallery density (Kruskal and Wallis 1952, Conover 1971, Zar 1984). When results were significant, nonparametric multiple comparisons were used to identify differences among species (Conover 1971, Zar 1984). All analyses were conducted at the $P < 0.05$ level of significance.

Results

Study 1: Adult Landing, Oviposition, and Larval Development on Cut Logs Attached to t-posts (2003)

Adult Landing. A total of 602 *A. planipennis* adults were collected from the 109 logs and 16 pieces of drain pipe that had sticky bands, ranging from 0 to 48 with a mean of 4.8 ± 0.7 beetles per log. Thirty-four percent of the beetles were caught on the six blocks of logs at Bicentennial Park, 33% on the four blocks at the Eckles yard, and 21% on the six blocks at Kensington Park. Only 12% of the beetles were captured on the eight blocks of logs at Western golf course, significantly fewer than the number captured at the other three sites ($F = 21.28$; df = 3,121; $P < 0.0001$). White ash and green ash logs captured 39% of all beetles, but differences in landing rates among log species were not significant (Table 1). Significantly fewer *A. planipennis* adults landed on drain pipes, which accounted for only 3% of the adults, than on ash, elm, walnut, and hickory logs ($F = 3.04$; df = 6,118; $P = 0.0091$; Table 1). Only a few adults were collected from hackberry logs; landing rates on hackberry did not differ significantly from the other logs or the drain pipes (Table 1). The interaction between site location and species was not significant ($P = 0.56$).

Oviposition. The number of eggs found in 5 min of searching ranged from 0 to 32 with a mean of 1.8 ± 0.3 eggs per log. On average, ≈8 times more eggs were found on ash logs than on all nonash logs combined (Table 1). Of the 256 eggs found, 78% were on ash logs. Fifty-five percent of the ash logs had eggs compared with 23% of the nonash logs (Table 1). Twelve of the 23 eggs found on walnut were on a single log at the Western golf course. No eggs were found on the drain pipes.

Egg density differed significantly among sites (H = 12.69; df = 3, 139; $P = 0.0054$) and log species (H = 31.18; df = 5, 137; $P < 0.0001$). Logs at Kensington Park had significantly higher egg densities than logs at Western golf course, whereas egg densities on logs at Bicentennial Park and the Eckles yard were intermediate. White ash logs had significantly more eggs per square meter than elm, walnut, and hickory logs (Table 1). There was a significant interaction between site

Table 2. Mean ± SE no. *A. planipennis* eggs per square meter and galleries per square meter for logs attached to *A. planipennis*-infested ash trees in 2003, 2004, and 2005

			Logs			
	Green ash	White ash	Black ash	Blue ash	American elm	Black walnut
2003—Logs attached to green ash trees						
No. logs	10	N/A[a]	N/A	N/A	10	10
No. logs with eggs	9	N/A	N/A	N/A	5	1
Total no. eggs	99	N/A	N/A	N/A	12	3
Mean no. eggs/m²	47.1 ± 15.8a	N/A	N/A	N/A	4.9 ± 2.4b	1.6 ± 1.6b
No. logs with galleries or feeding attempts	10	N/A	N/A	N/A	0	1
Total no. galleries	406	N/A	N/A	N/A	0	0
Mean no. galleries/m²	195.5 ± 49.5a	N/A	N/A	N/A	0b	0b
Total no. feeding attempts	0	N/A	N/A	N/A	0	3
Mean no. feeding attempts/m²	0	N/A	N/A	N/A	0	0
2004—Logs attached to white ash trees						
No. logs	18	9	N/A	9	9	9
No. logs with eggs	10	8	N/A	4	0	1
Total no. eggs	19	49	N/A	10	0	1
Mean no. eggs/m²	4.9 ± 1.3ab	28.1 ± 6.8a	N/A	5.2 ± 2.7ab	0b	0.6 ± 0.6b
No. logs with galleries or feeding attempts	14	9	N/A	6	0	0
Total no. galleries	75	266	N/A	28	0	0
Mean no. galleries/m²	17.0 ± 3.3b	143.6 ± 33.5a	N/A	14.0 ± 5.0bc	0c	0c
Total no. feeding attempts	0	0	N/A	0	0	1
Mean no. feeding attempts/m²	0	0	N/A	0	0	0
2005—Logs attached to green and white ash trees						
No. logs with galleries or feeding attempts	36	35	14	10	N/A	7
Total no. galleries	800	621	122	115	N/A	0
Mean no. galleries/m²	97.4 ± 13.3a	70.0 ± 8.9ab	39.6 ± 7.2b	42.2 ± 16.6b	N/A	0c
Total no. feeding attempts	0	0	0	0	N/A	148
Mean no. feeding attempts/m²	0	0	0	0	N/A	48.4 ± 19.8

Within rows, means followed by the same letter are not significantly different (Kruskal-Wallis test and nonparametric multiple comparisons procedure; *P* < 0.05).

[a] White ash, black ash, and blue ash were not included in 2003. Black ash was not included in 2004. American elm was not included in 2005.

and species ($F = 2.0$; df = 15,119; $P = 0.0208$), likely reflecting the very low egg densities on logs at the Eckles yard and Western golf course. When Eckles and Western were removed from the analysis, ash logs had significantly higher egg densities than elm, walnut and hickory logs; hackberry logs were intermediate ($H = 41.4$; df = 5,64; $P < 0.0001$).

Larval Development. A total of 432 *A. planipennis* larval galleries were excavated on 19 of the 47 green and white ash logs (Table 1). Number of galleries per ash log ranged from 0 to 75 with a mean of $9.2 ± 2.7$, but 70% of the ash logs had no more than four galleries. Green and white ash logs at Bicentennial Park had the highest gallery density with ≈110 galleries/m², compared with ≈50 galleries/m² at Kensington Park, 7 galleries/m² at Western, and 3 galleries/m² at Eckles. Most larvae reached the second or third instar before logs became too dry to sustain development.

Gallery density was significantly affected by site ($H = 11.65$; df = 3,139; $P = 0.0087$) and log species ($H = 45.77$; df = 5,137; $P < 0.0001$). There were significantly more galleries per square meter on logs at Bicentennial and Kensington parks than at Western golf course; gallery densities at Eckles were intermediate. Ash logs had significantly more galleries per square meter than the nonash logs (Table 1). The interaction was significant ($F = 4.79$; df = 15,119; $P < 0.0001$), again reflecting the low gallery densities on logs at Eckles yard and Western golf course and the relatively high densities at Bicentennial and Kensing-

ton parks. Of the 72 logs inspected from Eckles yard and Western golf course, only 39 galleries were excavated on three white ash logs. Results remained consistent when Eckles and Western were removed from the analysis; ash logs still had significantly more galleries than nonash logs ($H = 43.7$; df = 5,64; $P < 0.0001$).

Four walnut logs had discernable *A. planipennis* feeding attempts made by first-instar larvae (Table 1). Feeding attempts refer to galleries made by first-instar larvae that fail to develop and die. Of the 51 larval feeding attempts on walnut, 47 were on a single log and consisted of very thin galleries, <2 cm long. All larvae died as first instars. Elm, hickory, and hackberry logs had no feeding attempts (Table 1).

Study 2: Oviposition and Larval Development on Cut Logs Positioned in Ash Trees (2003, 2004, 2005)

2003. The number of *A. planipennis* eggs found in 5 min of searching ranged from 0 to 35 per log, with a mean of $3.8 ± 1.4$ eggs per log. Site location did not significantly affect egg density ($P = 0.41$), but density differed significantly among log species ($H = 15.45$; df = 2,27; $P = 0.0004$). *A. planipennis* females laid significantly more eggs per square meter on green ash logs than on walnut and elm logs (Table 2). The interaction between site and species was not significant ($P = 0.23$).

Overall, the mean number of galleries per green ash log was 40.6 ± 10.1. Nearly all larvae reached the second or third instar before logs became desiccated. Only three feeding attempts, each <1 cm long, were identified on 1 of the 10 black walnut logs. No galleries or feeding attempts were found on any of the elm logs (Table 2). Gallery density varied significantly among log species (H = 27.49; df = 2,27; $P < 0.0001$) but not among sites ($P = 0.36$), nor was the interaction significant ($P = 1.0$). Green ash logs had significantly more *A. planipennis* galleries per square meter than walnut and elm (Table 2).

2004. The number of eggs found in 5 min of searching ranged from 0 to 13, with a mean of 1.5 ± 0.4 eggs per log. Egg densities on white ash logs were almost five times that of other species, including green ash and blue ash (Table 2). Only one egg was found on walnut, and no eggs were found on elm. Egg density varied significantly among species (H = 23.79; df = 4,49; $P < 0.0001$) but not among sites ($P = 0.054$). White ash logs had significantly more eggs per square meter than elm and walnut logs, but egg density did not differ significantly among the three ash species (Table 2). The interaction between site and species was not significant ($P = 0.32$).

A total of 389 larval galleries were excavated on the three ash species. Gallery density varied significantly between sites (S = 618.0; df = 1,52; $P = 0.0115$). On average, there were almost five times more galleries per square meter on the logs at Parker Mills than the logs at Marshall Park. Gallery density also varied significantly among log species (H = 35.61; df = 4,49; $P < 0.0001$). White ash logs had significantly more galleries per square meter than the other species, with three times more galleries than the other ash species (Table 2). Only one small feeding attempt was found on a walnut log and no feeding attempts were found on elm (Table 2). The interaction between site and species was not significant ($P = 0.87$).

2005. *A. planipennis* larvae excavated 800 and 621 galleries on 36 green ash logs and 35 white ash logs, respectively (Table 2). We found 148 first-instar feeding attempts on 7 of the 12 black walnut logs. Results from the three-way ANOVA indicated that differences between street trees versus woodlot trees and between green ash versus white ash were not significant ($P = 0.0509$ and $P = 0.0604$, respectively). Gallery density did, however, vary significantly among log species (F = 16.23; df = 4,61; $P < 0.0001$). Green ash logs had significantly more galleries per square meter than black ash, blue ash, and black walnut logs, but gallery density in white ash logs did not differ significantly from the other ash logs (Table 2). None of the two-way interactions were significant, including site type by log species ($P = 0.07$), tree species by site type ($P = 0.38$), and tree species by log species ($P = 0.79$).

A significant three-way interaction occurred for tree species by site type by log species (F = 3.33; df = 4,61; $P = 0.0156$). Therefore, means were separated and analyzed within each site type and tree species. At the Wellington site with green ash street trees, there were significantly more galleries per square meter in the green ash, white ash, and black ash logs than on the walnut logs, which had no galleries (Fig. 1a). At the Kensington site, where logs were attached to green ash woodlot trees, green ash logs had significantly more galleries per square meter than blue ash, black ash, and walnut logs (Fig. 1b). At the Windemere site, where logs were attached to white ash street trees, green ash and blue ash logs had significantly more galleries per square meter than white ash, black ash, and walnut logs (Fig. 1c). At Dicken Woods, where logs were attached to white ash trees in a woodlot, the only significant difference was between the ash and walnut logs (Fig. 1d).

Study 3: Larval Density and Development on Live Trees (2004, 2005)

2004. Similar numbers of galleries were found on the upper portions of the green and white ash nursery trees in the Matthaei Botanical Gardens plantation (Table 3). A single larval feeding attempt was found on one Japanese tree lilac. No feeding attempts were found on black walnut trees. On average, green ash and white ash trees had 146.9 ± 46.3 and 76.5 ± 6.7 galleries/m², respectively (Table 3). Gallery density did not differ significantly between green and white ash trees, but the ash trees had significantly more galleries per square meter than tree lilac and walnut (overall H = 33.82; df = 3,36; $P < 0.0001$; Table 3).

Bark texture of ash trees seemed to be related to larval gallery density. Of the 1,258 galleries found on the 10 green ash trees (Table 3), 68% were on four trees with high bark roughness. The 10 white ash trees and six of the green ash trees had smooth bark, except for branch junctions where rough or fissured bark was usually present. Ash stems with rough bark had a mean of 458 ± 51 galleries/m², which was significantly more than the 137 ± 13 galleries/m² on ash stems with smooth bark (S = 74.0; df = 1,18; $P < 0.0001$). Bark on Japanese tree lilac trees was consistently rated as medium in texture, whereas all 10 black walnut trees had rough bark.

2005. Green ash trees had 365 more galleries than white ash trees (Table 3). We found two larval feeding attempts on one Japanese tree lilac and no feeding attempts on the black walnut trees. There were significantly more galleries on green ash and white ash trees than on tree lilac and walnut (H = 33.46; df = 3,36; $P < 0.0001$; Table 3). More than 70% of the galleries on green ash trees were on five trees with rough bark. Ten white ash and the other five green ash trees had smooth bark. Ash stems with rough bark and ash stems with smooth bark had a mean of 255 ± 26 and 163 ± 21 galleries/m², respectively, and differences in gallery density were significant (S = 80.0; df = 1,18; $P < 0.0146$).

Study 4: American Elm Survey

All nine elm trees that were felled and debarked appeared healthy. A total of 28.4 m² of elm surface area
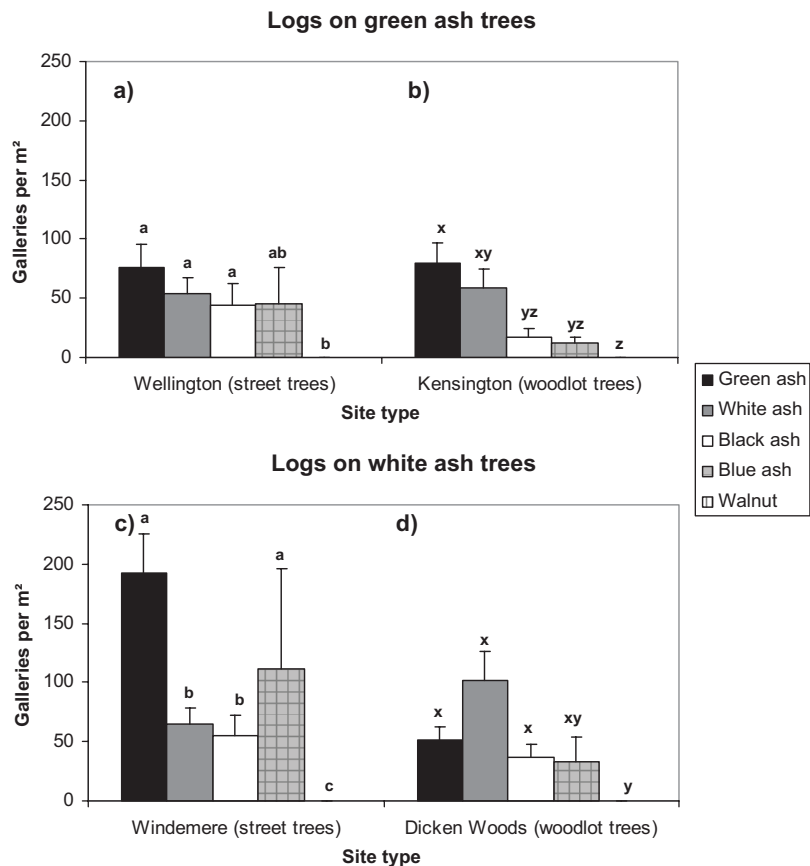
Fig. 1. Mean (±SE) number of *A. planipennis* galleries per square meter on logs of five species attached to *A. planipennis*–infested (a) green ash street trees, (b) green ash woodlot trees, (c) white ash street trees, and (d) white ash woodlot trees in 2005. Within site type and tree species, means with the same letter are not significantly different (Fisher protected LSD test; *P* < 0.05).

was sampled, averaging 3.2 ± 0.5 m² per tree. There was no evidence that any *A. planipennis* ever fed or attempted to feed on the elms despite the proximity of the heavily infested ash trees. No other signs of insect colonization or pathogen infection were apparent on any of the elms.

Table 3. Mean ± SE tree DBH, surface area sampled per tree and total and mean ± SE no. *A. planipennis* galleries per square meter for four species of nursery trees in 2004 and 2005

	Green ash	White ash	Japanese tree lilac	Black walnut
2004 nursery trees				
No. trees	10	10	10	10
DBH (cm)	6.0 ± 0.2	6.3 ± 0.2	4.6 ± 0.1	6.4 ± 0.2
Mean surface area sampled (m²)	0.46 ± 0.09	0.73 ± 0.07	0.26 ± 0.02	0.56 ± 0.03
Total no. galleries	535	522	0	0
Mean no. galleries/m²	145.7 ± 46.6a	76.5 ± 6.7a	0b	0b
Total no. feeding attempts	0	0	1	0
Mean no. feeding attempts/m²	0	0	0.4 ± 0.4	0
2005 nursery trees				
No. trees	10	10	10	10
DBH (cm)	8.0 ± 0.2	7.5 ± 0.2	5.3 ± 0.1	7.7 ± 0.2
Mean surface area sampled (m²)	1.98 ± 0.27	1.71 ± 0.09	0.31 ± 0.03	0.61 ± 0.03
Total no. galleries	1258	893	0	0
Mean no. galleries/m²	58.9 ± 10.0a	51.6 ± 2.7a	0b	0b
Total no. feeding attempts	0	0	2	0
Mean no. feeding attempts/m²	0	0	0.5 ± 0.5	0

Within rows and years, means followed by the same letter are not significantly different (Kruskal-Wallis test and nonparametric multiple comparisons procedure; *P* < 0.05).

Discussion

Host range expansion or host shifting by phytophagous insects has been previously documented, most commonly with polyphagous foliage-feeders (Strong 1979, Strong et al. 1984, Claridge and Evans 1990, Bush 1994). Changes in host range can occur when, for example, a phytophagous insect population encounters new hosts that are similar architecturally, phenologically, or chemically to their original hosts (Fraser and Lawton 1994) or because a novel host provides the phytophage with enemy-free space (Rossbach et al. 2006). Our studies, which addressed the ability of *A. planipennis* to use North American congeners of hosts reportedly attacked in Asia, represent a somewhat unique aspect of insect–host plant relationships. We initiated our studies in May 2003, less than 1 yr after *A. planipennis* was discovered in North America. Little information about *A. planipennis* biology or ecology was available at the time of its discovery (Cappaert et al. 2005b). We did, however, have access to taxonomic descriptions of *A. planipennis*, *A. planipennis* subsp. *ulmi*, *A. marco-poli*, and *A. marco-poli ulmi*, all of which were synonymized into *A. planipennis* by Jendek (1994). The taxonomic papers included brief lists of hosts colonized in Asia, which included several Asian *Fraxinus* spp., along with Asian species of *Ulmus*, *Juglans*, and *Pterocarya* (Kurosawa 1956, Chinese Academy of Science 1986, Yu 1992, Akiyama and Ohmomo 1997, 2000).

Our primary goal was to determine whether *A. planipennis* adults would land on or oviposit on the nonash hosts, and if so, whether larvae could successfully develop on these species. If *A. planipennis* host range extends beyond *Fraxinus* spp., the impacts of this invasive pest in North American forests would increase dramatically. Our second objective was to evaluate potential differences in *A. planipennis* preference among North American ash species commonly found in southeast Michigan.

Overall, we found that, although *A. planipennis* adults will occasionally land on and oviposit on logs and trees of nonash species, *A. planipennis* larvae did not successfully develop on anything other than *Fraxinus* species. Study 1 featured arrays of similarly sized logs of ash and potential alternate hosts mounted on t-posts, all located at least several meters from ash foliage. Landing rates of *A. planipennis* adults were not strongly influenced by log species, but female beetles were apparently able to distinguish between ash and nonash logs during oviposition; nearly 80% of the eggs we recovered were on ash logs. We have since learned that female *A. planipennis* must feed on ash leaves for at least 2 wk before oviposition begins (Bauer et al. 2004). Although some beetles that emerged from ash material at the Eckles disposal yard landed on our logs, the lack of available ash foliage precluded oviposition and most beetles likely dispersed to find leaves for feeding. Other species of *Agrilus* similarly require maturation feeding on foliage before oviposition (Carlson and Knight 1969). Beetles did avoid the plastic drain pipes, presumably because of the lack of ash volatiles,

texture, or other factors (Kimmerer and Kozlowski 1982, Dunn et al. 1986a, 1986b).

Our ability to find *A. planipennis* eggs in this and other studies varied among log species and depended largely on bark texture. Bark of some species, like hackberry, lacked flaky layers of periderm, and eggs were apparent because they were on the surface. Other species, including ash, required meticulous examination and careful removal of the flaky, outer layers of bark to reveal eggs hidden below the outer bark flakes. On ash, *A. planipennis* egg densities often were lower than larval gallery densities for this reason.

In study 2, the logs attached to the trunk of live ash trees, within or just below the lower canopy of the trees, were presumably surrounded by ash volatiles and ash foliage was readily available for maturation feeding. We hypothesized that if female *A. planipennis* laid eggs on the nonash logs, either by chance or because they could not distinguish between the ash and nonash logs, we could compare larval development among the log species. Results from all 3 yr showed that female beetles were very good at discriminating among log species. Although ovipositional "mistakes" did occur (e.g., oviposition on elm or black walnut logs), they were rare. Larvae that hatched from eggs laid on black walnut logs sometimes tried to feed, but none were able to grow, develop, or survive.

Results from study 3, where young trees established in a common plantation were exposed to high densities of *A. planipennis*, were similar. In this study, beetles were presented with live trees with foliage and intact vascular systems instead of cut logs, where moisture loss or altered defensive chemistry could have influenced larval development (Haack and Slansky 1986, Hanks 1999, Hanks et al. 1999). In both years, the ash trees were heavily colonized by *A. planipennis.* There were no *A. planipennis* galleries or feeding attempts on any of the black walnut nursery trees and only three small, unsuccessful feeding attempts, each ≈1 mm wide and 1–3 cm long, on two Japanese tree lilacs. In related studies with the same alternate host species conducted under no-choice conditions in the laboratory and field, we similarly found no evidence of larval development on anything other than ash species (Anulewicz et al. 2006).

Southeast Michigan represents a host suitability experiment on a grand scale; an estimated 20 million ash trees in this area had succumbed to *A. planipennis* by 2006 (www.emeraldashborer.info). To date, however, there is no evidence of *A. planipennis* attacking nonash trees. Since 2002, we have studied several anecdotal accounts of *A. planipennis* infestation in nonash trees, typically reported by landscapers or arborists. In every instance, either the tree was actually an ash tree that was misidentified or a nonash tree had been colonized by native scolytids, cerambycids, or buprestids. At the Bicentennial Park woodlot, where heavily infested green ash trees grew in close proximity or in direct contact with American elm trees, *A. planipennis* beetles had an opportunity to intentionally or accidentally oviposit on live elms. In some cases, larvae would have been able to feed from ash directly into elm with little

or no exposure. Although we intensively examined >28 m^2 of elm phloem, there was no sign that any *A. planipennis* larvae ever attempted to feed on the elms.

If the four *Agrilus* species or subspecies that were synonymized by Jendek (1994) are, in fact, a single species, *A. planipennis* clearly has the potential to use nonash hosts in North America. Whether this potential is realized, however, may depend on founder effects and the extent of genetic variability represented by the colonists that became established. An alternative explanation is that at least some of the beetles that were synonymized differ in their ability to recognize or develop on nonash hosts. As yet, the geographic origin of the *A. planipennis* population in North America is not known, nor can we say with certainty that the *A. planipennis* infestations in the United States and Canada are a result of a single introduction (Bray et al. 2005). Although it remains unclear how host range varies among subspecies or geographically distinct *A. planipennis* populations in Asia, a founder effect associated with an accidental introduction of a relatively low number of colonists could serve to limit *A. planipennis* to ash in North America. Additional research to identify the origin of the North American *A. planipennis* population and to determine whether *A. planipennis* from North American can develop in Asian species of *Juglans*, *Ulmus*, or *Pterocarya* could help to resolve these questions.

North American Ash Species

Agrilus planipennis did seem to exhibit a preference among the North American ash species included in our studies. In study 3, live green and white ash trees in our plantation were exposed to high densities of *A. planipennis* in both 2004 and 2005. Native and ornamental ash trees in the vicinity of the plantation began to succumb to *A. planipennis* in 2004, and by 2005, the 20 ash trees in our plantation were likely the only live ash trees within a 1.5-km radius. In both years, galleries on the green ash trees, particularly those with rough bark, were so dense that virtually all phloem was consumed. Similarly, when sites with both green and white ash trees were surveyed in southeast Michigan, green ash trees consistently had more canopy dieback and higher densities of *A. planipennis* than white ash trees (Anulewicz et al. 2007a). Most larvae on the green ash trees in our plantation died before reaching the fourth instar because of intraspecific competition. We observed similarly high attack rates and larval mortality on other ash trees in the field (McCullough and Siegert 2007).

Study 2, where logs were attached to the trunks of ash trees in heavily infested areas, provided an opportunity to assess differences in *A. planipennis* host preference among North American ash species, as well as suitability of nonash species. Results from 2003, where green ash logs were attached to green ash trees were relatively straightforward; green ash logs consistently had high larval densities. In 2004, however, when both green and white ash logs were attached to white ash trees in wooded areas, gallery densities were

considerably lower in the green ash than in the white ash logs. Although highly debated, Hopkins' host selection principle is based on observations that show many adult insects demonstrate a preference for the host species on which they themselves developed as larvae (Barron 2001). We hypothesized that host conditioning may have influenced *A. planipennis* oviposition in 2004, because most beetles that oviposited on our logs likely emerged from white ash trees. Therefore, we repeated the study in 2005, but attached both green and white ash logs to green and white ash trees. If a conditioning effect had occurred, we expected gallery densities in green ash logs would be higher when logs were attached to green ash trees than white ash trees. Similarly, larval density in white ash logs should be higher when logs were attached to white ash trees than to green ash trees. Results, however, were not consistent with a conditioning effect. At three of the four sites, green ash logs had more galleries per square meter than white ash logs, although differences were statistically significant only at the Windemere site, where the logs were in white ash street trees. Other factors, including the apparent preference of *A. planipennis* adults for sunny locations or subtle differences in log quality, may have influenced the 2004 results.

Blue ash logs were included in study 2 in 2004 and 2005, and black ash logs were included in 2005. Blue ash logs were apparently not highly attractive to ovipositing beetles, but larvae on blue ash and black ash logs developed normally. We have observed full development and emergence of *A. planipennis* on black ash and blue ash trees in the field, so there is no question that these species are suitable hosts. What is unclear is the order of preference among all four species, whether this preference is consistent, and how host preference is modified by factors such as *A. planipennis* density, exposure of host trees to sun, or physical traits of trees. Sunny, open conditions, for example, seem to be more attractive to *A. planipennis* beetles than shaded locations within closed canopy woodlots (Poland et al. 2005, Francese et al. 2006, McCullough et al. 2006, Anulewicz et al. 2007b), a behavior noted for some native *Agrilus* sp. and other buprestids (Barter 1957, Carlson and Knight 1969). In addition, *A. planipennis* females, as well as females of other *Agrilus* species, may prefer rough-barked portions of trees for oviposition (Barter 1957, Loerch and Cameron 1984), where eggs may be more likely to escape physical stress or predation. Additional research is needed to assess how physical characteristics of hosts and variation in the abundance and chemical profile of volatiles among ash species affect *A. planipennis* oviposition and development.

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